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A Biometrical Study of Conjugation in Paramæcium.

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(Abstract.)

1. A study of variation and correlation in conjugating and non-conjugating specimens of the common ciliate infusorian, *Paramæcium caudatum*, was undertaken for the purpose of obtaining answers to the following questions:—

a. Is the portion of the *Paramæcium* population which is in a state of conjugation at a given time differentiated in respect of type or variability or both from the non-conjugating portion of the population living in the same culture at the same time?

b. Is there any tendency for like to pair with like ("homogamy") in the conjugation of *Paramæcium*, and if so, how strong is this tendency?

The material on which this paper is based is comprised in eight series, taken from three different cultures at different times, and includes altogether the measurements of 1894 individual *Paramæcia*. The characters studied were length and greatest breadth of the body, length-breadth index, and the difference in length between the two individuals of a pair of conjugants. In the measuring conjugant pairs were taken quite at random, and then in each case the two undistorted non-conjugant individuals which were lying nearest in the field of view of the microscope to the conjugant pair were measured. This procedure was followed to avoid any sub-conscious bias in choosing non-conjugants.

The cultural history of the different series may be summarised as follows:—

Series A, C, D, and E.—These series all came from a single culture in the Zoologisches Institut, at Leipzig. This culture was set with dry hay and pond water, July 25, 1905. The dates of collection and measurement and number of individuals in each series are given in the table on p. 378.

Series B.—This series came from another culture at Leipzig set in the same manner as the one just mentioned. Conjugants were found on August 22, but in very small numbers. On the next day only two pairs of conjugants were found, and after that none at all. So that, all told, Series B included only 12 pairs of conjugants and 24 non-conjugants.

Series AA, F_E, and F_L.—These series included only conjugants. They were

measured from material in the Zoological Laboratory of the University of Michigan, collected by Professor D. C. Worcester. They all came from a single culture set with decaying plant material and pond water. Series AA includes 200 pairs of conjugants, Series F_E 70 pairs, and Series F_L 77 pairs.

Series.	Dates of measurement.	Number of conjugants measured.	Number of non-conjugants measured.
A	August 15, P.M.—August 18, noon, inclusive	105 pairs	210
C	„ 24, A.M.— „ 26, P.M., „	101 „	202
D*	„ 30.....	16 „	32
E	September 6	—	132

For further details regarding the measurements, culture histories, etc., the complete paper must be consulted.

2. An examination of the variation constants shows that Paramæcium is relatively slightly more variable in breadth than in length of body, though the difference is not large. For the variation in length the coefficients of variability for different series (including several other long series besides those collected in this work) are found to cluster well together about a value of 8 to 9 per cent. This is a much lower value than has been found by other workers† for variation in similar size characters in organisms with firm exoskeletons. In the characters studied Paramæcium follows the same general laws which have been shown to hold for continuous variation in higher forms.

3. It was found that conjugants are markedly differentiated from non-conjugants living in the same culture in both type and variability. This differentiation includes all the characters studied. An idea of its extent and direction may be gained by an examination of the following table. In it are given (*a*) the absolute differences between conjugants and non-conjugants in respect to the character and constant designated; (*b*) the probable errors of these absolute differences; (*c*) the relative differences defined as the percentage which the absolute difference is of the non-conjugant constant in each case. The absolute differences are taken as positive when the non-conjugant constant is greater. Only two series (A and C) are taken here as illustrations. In the complete paper similar data for other series are given in detail.

* Series D and B (*vide infra*) include only a few individuals, because at the time they were collected no more conjugants were to be found in the cultures from which they came.
† For detailed references, see complete paper.

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Table I.—Differentiation of Conjugants from Non-conjugants.

Series.	Character.	Constant.	Absolute difference between non-conjugants and conjugants.	Relative differ- ence between non-conjugants and conjugants.
A	Length	Mean	21·833 $\pm$ 0·893 micron	Per cent. 11·5
		Standard deviation ...	4·337 $\pm$ 0·631 "	27·9
		Coefficient of variation	1·517 $\pm$ 0·349 per cent.	18·5
	Breadth.....	Mean	8·456 $\pm$ 0·335 micron	16·0
		Standard deviation ...	1·700 $\pm$ 0·237 "	28·96
		Coefficient of variation	1·714 $\pm$ 0·484 per cent.	15·4
	Index.....	Mean	1·510 $\pm$ 0·171 "	5·4
		Standard deviation ...	-0·195* $\pm$ 0·121 "	7·8
	Length and breadth	Coefficient of correla- tion	0·3107 $\pm$ 0·0526	52·7
C	Length	Mean	33·341 $\pm$ 1·098 micron	15·9
		Standard deviation ...	6·005 $\pm$ 0·777 "	31·4
		Coefficient of variation	1·684 $\pm$ 0·398 per cent.	18·5
	Breadth.....	Mean	11·050 $\pm$ 0·324 micron	20·4
		Standard deviation ...	2·491 $\pm$ 0·229 "	42·2
		Coefficient of variation	2·984 $\pm$ 0·456 per cent.	27·4
	Index.....	Mean	1·416 $\pm$ 0·155 "	5·5
		Standard deviation ...	-0·152* $\pm$ 0·110 "	6·8
	Length and breadth	Coefficient of correla- tion	0·4072 $\pm$ 0·0542	66·4

This table shows that the differentiation between conjugants and non-conjugants is strikingly large in both type and variability for all characters. The same is true for the organic correlations between length and breadth. The conjugant individuals, when compared with non-conjugants, are found to be shorter and narrower, and less variable in both length and breadth. The conjugants have a lower mean index—or, in other words, are relatively more slender—and are more variable in shape of body, as indicated both by length-breadth index and by the organic correlation between length and breadth. The conjugants have the length and breadth less highly correlated than the non-conjugants.

4. To determine whether there was any definite tendency for like to pair with like (homogamy) in the conjugation of *Paramaecium*, the correlation between the two members of conjugant pairs was determined for (a) the

* The higher variability of the length-breadth index in the conjugants really arises from the fact that the organic correlation between length and breadth is much lower in conjugants than in non-conjugants.

same character in each member, *e.g.*, length of A with length of B (direct homogamic correlation), and (b) a different character in each member, *e.g.*, length of A with breadth of B (cross homogamic correlation). A part of the results for direct homogamy in respect to the character length are shown in Table II.

Table II.—Direct Assortative Pairing in the Conjugation of *Paramecium*.
Lengths only.

Series.	Characters.		Coefficient of correlation.	Number of pairs.
A	Length of A*	Length of B*	0·5327 ± 0·0333	105
C	" A	" B	0·7249 ± 0·0225	101
D	" A	" B	0·4302 ± 0·0972	16
B	" A	" B	0·7941 ± 0·0509	12
AA	" A	" B	0·5882 ± 0·0221	200

It will be seen that these coefficients are relatively very high. The only quantitative determinations of the degree of homogamy in any organism which have hitherto been made, are those for assortative mating in man, made by Pearson and his collaborators.† For the characters so far investigated in man, the coefficients of direct homogamy fall uniformly below 0·3. It is evident that we are dealing here with a much more intense assortative pairing.

For the other characters, breadth and index, the direct homogamic correlations are not so high as for length, though still relatively large. Taking the means of the results for the different series, I find for the direct homogamic correlation of breadth with breadth $r = 0·3028$, and for the correlation of index with index $r = 0·4291$.

The cross homogamic correlations (length of A with breadth of B and *vice versa*) were found to be low in all cases. The average value of the coefficients for these cross correlations was 0·1082.

It will be noted that the homogamic correlations are in all cases positive.

5. In order to test whether the observed homogamic correlations were real or spurious, various sorts of random pairings were tried. The first question which might be raised is as to what would be the value of the coefficients measuring homogamy, provided we experimentally paired together conjugants or non-conjugants quite at random. This has been done several times for

* A and B refer respectively to the first and second individuals of a conjugant pair to be measured.

† 'Biometrika,' vol. 1, p. 373, and vol. 2, pp. 481—498.

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each series of measurements with entirely uniform results. The coefficients, measuring direct homogamy in random pairs of (*a*) conjugants; (*b*) non-conjugants; or (*c*) pairs in which one member is a conjugant and the other a non-conjugant, are uniformly zero within the limits of the probable errors.

It might be maintained that since at different points in the culture and at different times the environment no doubt differs slightly, there would be a corresponding differentiation of the Paramæcia in each local unit of the culture. Then even though the pairing were really quite at random in each locality, yet if the records for several such localities were mixed, a spurious homogamic correlation would arise. Now it is clear that if the observed homogamic correlations were spurious and due to this "local differentiation" factor, we ought to get sensibly as high values if we consider as a pair the two individuals lying nearest in the field of view to each pair of conjugants measured. Such pairs will have come from the same environment and have been killed at the same instant as the actually conjugated pairs. The homogamic correlations for these pairs of individuals, lying nearest to conjugant pairs, have been determined and found to be sensibly zero, taking into account their probable errors. This I take to prove that the observed homogamic correlations are not to be explained as due to local differentiation within the culture.

6. The existence of a high degree of assortative pairing with respect to length can be shown in another way. We may consider as a character of conjugant pairs the difference in length between the two members. Forming frequency distributions of this difference for (*a*) conjugated pairs; (*b*) random pairs of conjugants; and (*c*) random pairs of non-conjugants (the two individuals lying nearest each conjugant pair measured), I find that the mean difference in microns is from two to three times greater in the random pairs—whether of conjugants or non-conjugants—than it is in the actually conjugated pairs. In more than 60 per cent. of the conjugated pairs, the two members differ in length by less than 8 microns. There is a much greater "scatter" of the variates about the mean in the case of the random pairs as compared with the conjugated pairs. These results for the difference distributions are, of course, what would be expected if there is a high degree of homogamy in respect to length.

7. In order to determine whether the observed homogamic correlations are due to a real "assorting" in the pairing, or, on the other hand, arise from some process of equalisation in size occurring after union has taken place, the following test was made:—Two series of conjugants were measured and the homogamic correlations calculated. In the first of these series were included only pairs which were known, on the basis of their nuclear condition,

to be in very early stages of the conjugation process. In the second series were included only pairs which, on the same basis of nuclear condition, were known to be about to separate shortly. Now if the observed homogamy is a result of an equalisation of the members of the pairs in size during the conjugation process itself, clearly the second of these two series ought to show the higher homogamic correlations, because the individual pairs are in late stages, and we should expect to get the maximum effect of any equalisation which had occurred. As a matter of fact the coefficients of direct homogamy in length are 0.6797 ± 0.0307 for the "early" series and 0.6212 ± 0.0334 for the "late" series. The coefficients are sensibly equal for the two, with what advantage there is in favour of the "early" rather than the "late" series. From this it is concluded that the observed homogamy is not due to an equalisation in size during the conjugation process itself.

8. From evidence which is discussed in detail in the complete paper, it appears probable that the observed homogamic correlations arise as the result of a process, the essential factors in which may be outlined as follows: (a) At the periods of conjugation the individuals which are to conjugate are in a so-called "miscible" condition in which the oral surfaces are adhesive; (b) as a result of the action of the currents, produced by the oral groove cilia, two individuals which by chance happen to be swimming parallel and close to one another are drawn together and their oral surfaces adhere in whole or in part; (c) the extreme anterior ends of the oral grooves *firmly* adhere to one another first; (d) if the two individuals are so nearly the same size that the mouths approximately coincide when the anterior ends are together, firm union occurs at the mouth regions, and definite conjugation follows; (e) if, on the other hand, the mouths do not approximately coincide, the individuals separate again or die, and no conjugation results; (f) the homogamic correlations arise then as a result of the necessity for the mouths of the two individuals to come together (or "fit") when the extreme anterior ends are united. Individuals in which the distances from the anterior end to the mouth are approximately equal, will not be greatly different in total length, and hence their lengths will be correlated. The direct homogamic correlations for breadth and index, and the cross homogamic correlations, are held on this view to have arisen because of the organic correlation between length and breadth in the individual.

9. In concluding, some of the theoretical bearings of the work are discussed. It is pointed out that if the results obtained in this work with reference to the existence of a differentiated "conjugant type" are true, they

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are of considerable significance in connection with current views regarding the theoretical relation of the Protozoa to evolutionary problems. The results show clearly that, so far as the present material is concerned at least, (*a*) there is a differentiated "conjugant type" of *Paramæcium*; and (*b*) that this "conjugant type" is relatively fixed and constant under varying environmental conditions, as compared with the type of the general population in fission generations. If the individual *Paramæcia* of a given race must conform to a definite and relatively fixed morphological type every time they conjugate, what they may acquire during fission generations is clearly of no particular account to the evolutionary history of the race in the long run. Real evolutionary progress will depend on changes in the "conjugant type," just as in the Metazoa real evolutionary progress depends on changes in the germ cells rather than in the soma.

Attention is called to the significance which a high degree of homogamy, whenever it exists, must have as a factor in divergent evolution. A high degree of homogamy furnishes at once the means whereby a new variety or species may be differentiated from a parent species, though both continue to live together in the same area or environment. Because, if like mates with like, with any considerable regularity or uniformity, whenever individuals appear showing deviations from the general population, those which have on the whole like deviations will tend to mate together rather than with individuals unlike themselves belonging to the parent stock. Hence, the variations will not be "swamped by intercrossing" before natural selection has an opportunity to act on them. Hitherto, the existence of a high degree of homogamy has not been demonstrated quantitatively in any organism living in a state of nature. The results of the present work show that not only is such a degree of homogamy possible under natural conditions, but that it actually exists in one case of what must be considered as the simplest forerunner of the sexual processes of higher organisms, namely, the conjugation of a protozoon.